

NEW SPECIES OF SALAMANDERS (GENUS *BOLITOGLOSSA*) FROM
COLOMBIA, ECUADOR AND PANAMÁ

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ABSTRACT: Several undescribed species of plethodontid salamanders are reported from South America and Panamá. *Bolitoglossa medemi* is a dark species with rather large, extensively webbed hands and feet and a broad head. It is known from several sites in northwestern Colombia and extreme southwestern Panamá, where it occurs between 50 and 800 m elevation. *Bolitoglossa ramosi* is a somewhat smaller species, with lighter coloration, small but extensively webbed hands and feet, and a broad head. It occurs in sympatry with *Bolitoglossa valleculea* in the Cordillera Central east of Medellín, Colombia, at elevations of about 1930 m. *Bolitoglossa silverstonei* is a slender, long-tailed species with light pigmentation, broad and extensively webbed hands and feet, and a head of moderate breadth. It is known only from a site near Quibdo, in northwestern Colombia, at an elevation of 400 m. *Bolitoglossa walkeri* has less extensively webbed hands and feet and fewer maxillary teeth than the other species. It has dark dorsal and light ventral coloration. This species occurs near Cali, Colombia, at elevations near 2000 m. *Bolitoglossa equatoriana* has more extensively webbed hands and feet than *B. walkeri*, but shares similar low numbers of teeth and coloration. It occurs sympatrically with *B. peruviana* at elevations of about 260 m in Amazonian Ecuador. These new species permit a re-evaluation of relationships among South American members of the genus *Bolitoglossa*. Characters used for analysis of relationships among the twenty-two species are discussed, and five species groups are recognized. The *palmata* and *altamazonica* groups are divided. *B. silverstonei* is assigned to a new *sima* group, along with *B. sima*, *B. chica*, and *B. biseriata*. The other newly described species are the only members of the *medemi* group.

Salamanders from the Neotropics have been known for over 140 years, but until recently they have been considered to be rare and insignificant. However, it is increasingly evident that the salamander fauna of the New World Tropics is extensive and diverse. The plethodontid salamanders, which range from northern Mexico to Bolivia, account for over 40 percent of all salamander species. This diverse group is of interest to evolutionary biologists

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in that it provides an opportunity to analyze an adaptive radiation in great detail. Many generalized salamanders, probably similar to ancestral forms, survive in extratropical habitats. In addition, many populations intermediate between adaptive extremes are known to occur in the tropics.

A major hindrance to intensive analysis of evolutionary patterns has been the absence of basic biological information concerning the tropical species. Most are poorly known, and are represented in collections by only a few specimens. For some areas, our knowledge of species composition is fragmentary and new populations continue to be discovered. One such area is northwestern South America where the known fauna has increased from one (Dunn, 1926) to nearly twenty species in recent years. In this paper we describe five additional species and discuss the relationships of South American members of the genus *Bolitoglossa*.

Many specimens used for this study were provided by Philip A. Silverstone, who collected salamanders incidental to his work with Colombian frogs. Brame obtained additional specimens in Colombia in the spring of 1971 and W. R. Heyer collected a fine series in Ecuador in the summer of 1971. These specimens are deposited in the Los Angeles County Museum of Natural History (LACM). Specimens also have been loaned to us by the following curators and museums: Charles F. Walker, University of Michigan, Museum of Zoology (UNMZ); Hobart M. Smith and Dorothy M. Smith, University of Illinois Museum of Natural History (UIMNH); William E. Duellman, University of Kansas Museum of Natural History (KU). Additional material is deposited at the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). We thank these curators and institutions for their assistance. We are grateful to William F. Presch for assistance in providing x-rays, and Les Siemens and Gene Christman for assistance with illustrations. Carlos Martinez provided the Spanish summary. Aspects of the work have been supported by NSF grant GB 17112 to David B. Wake.

The first species occurs in low coastal mountains of northeastern Colombia and neighboring Panamá. We are pleased to name it in honor of our good friend, Professor Federico Medem, of the Universidad Nacional de Colombia (Villavicencio), who has aided and encouraged us in our studies of Colombian salamanders.

Bolitoglossa medemi, new species

Figures 1 and 2

Holotype.—LACM 42276, an adult female from Finca Chibigúí, approximately 76° 30' W, 6° 15' N, on the Río Arquía, Departamento de Antioquia, Colombia. The specimen was collected on April 23, 1968, by Philip A. Silver-

stone, Jorge E. Ramos, and Nacianseno Borja. It was active on the ground during daylight hours. Elevation approximately 300 m (980 ft).

Paratypes.—COLOMBIA: LACM 42277-78, same data as holotype; PAS 237 (cleared and stained, LACM 72067), Belén, downstream from Finca Chibigúí, and very near Vegaes on the Río Arquía, Dept. Antioquia, about 100 m (328 ft) elevation; LACM 42280, along trail between Río Opogodó and Río Napipí, near the latter, approximately 77° 10' W, 6° 43' N, Dept. Chocó, 30 to 80 m (100-260 ft); LACM 42279, along Río Opogodó at base of eastern slope of the Serranía de Baudó, approximately 77° 18' W, 6° 50' N, Dept. Chocó, about 60 m (200 ft); LACM 70565, N slope Alto de Buey, Dept. Chocó, 400 m (1312 ft); LACM 70566, Camino de Yupe, Dept. Chocó, 350 m (1148 ft); LACM 70567, Camino de Yupe, Dept. Chocó, 400-500 m (1312-1640 ft); LACM 70568, Camino de Yupe, Dept. Chocó, 605 m (1984 ft). PANAMÁ: KU 116533-34, Río Jaque, 1.5 km above Río Imamadó approximately 77° 57' W, 7° 25' N, Prov. Darién, 50 m (164 ft); KU 116530, Jaque-Imamado divide in Cordillera de Jurado, above Río Jaque, Prov. Darién, 730-800 m (2394-2625 ft).

Diagnosis.—A moderately small species (5 adult males: 33.7–46.7, mean 40.4 mm SL [standard length, measured from tip of snout to posterior angle of vent]; 5 adult females: 34.2–48.2, mean 43.3 mm SL) with moderate numbers of maxillary (mean 41) and vomerine (mean 31) teeth. Distinguished from *B. ramosi* by having fewer maxillary teeth and a darker dorsal ground color; from *B. walkeri* by its broader head, more extensively webbed feet, and longer legs; from *B. equatoriana* by its more numerous maxillary teeth and somewhat longer legs. *Bolitoglossa medemi* is distinguished from other Panamanian and South American species by the combination of large, extensively to completely webbed hands and feet, relatively broad head, long legs, distinctive coloration (very dark, unmarked dorsum, much lighter venter with a few widely scattered, irregular light pigment spots), and size and dentitional features (Table 1).

Description of Holotype.—Adult female with moderately long, somewhat pointed snout and small nostrils. Labial protuberances of nasolabial grooves small, poorly developed. Moderately long canthus rostralis gently arched. Head broad (SL 5.8 times head width) and moderately long (SL 4.2 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Large eyes slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 2.2 mm, then sharply ventrad at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 4.8 mm anterior to sharply defined gular fold. Vomerine teeth number 23, arranged in single rows that extend to lateral borders of internal nares; rows form slightly curved arches that terminate in center of palate, where they nearly meet. Small maxillary teeth number 41; extend posteriorly to point about two-thirds through eye. No premaxillary

teeth can be seen. Relatively short tail (0.75 times SL) has strong lateral compression and is moderately constricted at base. Postiliac glands poorly developed. Limbs long with limb interval (costal folds between appressed limbs) of one; SL 4.0 times right forelimb, 4.0 times right hind limb, 10.0 times right foot width. Webbing of hands and feet nearly complete, but all digital tips extend beyond thin web. Longest digits with long, pointed tips (Fig. 2). Large hands and feet; rather narrow and long compared with those of other extensively webbed species. No subterminal pads. Fingers, in order of decreasing length, 3, 4, 2, 1; toes, in order of decreasing length, 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 8.3; snout to gular fold (head length), 11.5; head depth at posterior angle of jaw, 4.0; eyelid length, 3.4; eyelid width, 2.2; anterior rim of orbit to snout, 3.7; horizontal orbital diameter, 2.6; interorbital distance, 3.0; distance between vomerine teeth and parasphenoid tooth patch, 0.8; snout to forelimb, 15.5; distance separating internal nares, 2.1; distance separating external nares, 2.7; snout projection beyond mandible, 0.8; snout to posterior angle of vent (SL), 48.2;

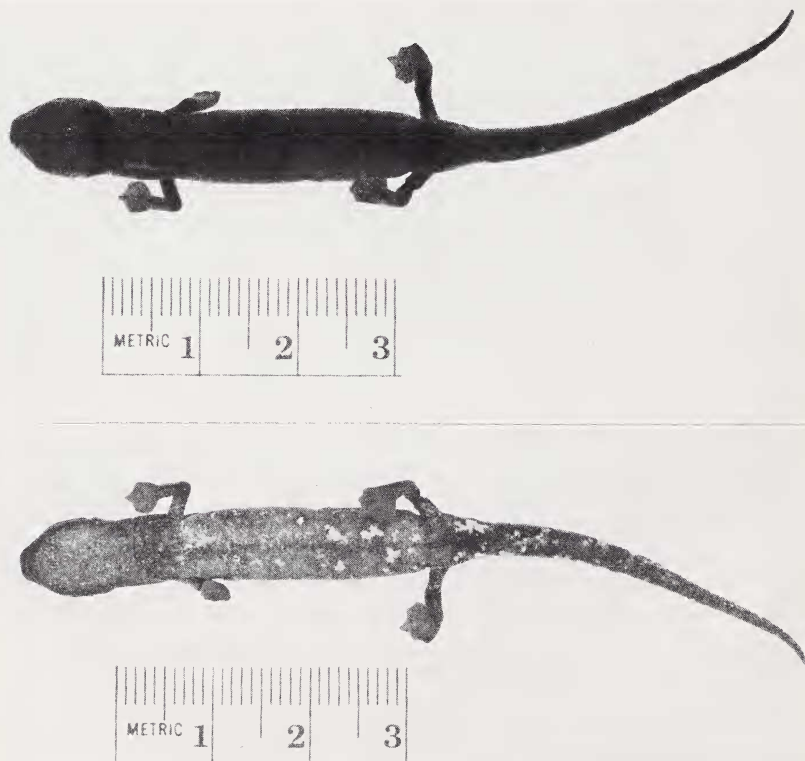


FIGURE 1. Dorsal and ventral views of holotype of *Bolitoglossa medemi* (LACM 42276).

snout to anterior angle of vent, 44.9; axilla to groin, 26.6; tail length, 36.3; tail width at base, 3.0; tail depth at base, 3.7; forelimb length, 12.2; hind limb length, 12.2; width of right hand, 3.6; width of right foot, 4.8.

Coloration of Holotype (in alcohol).—This is a very dark salamander which has the dorsum and upper two-thirds of the lateral sides of the trunk

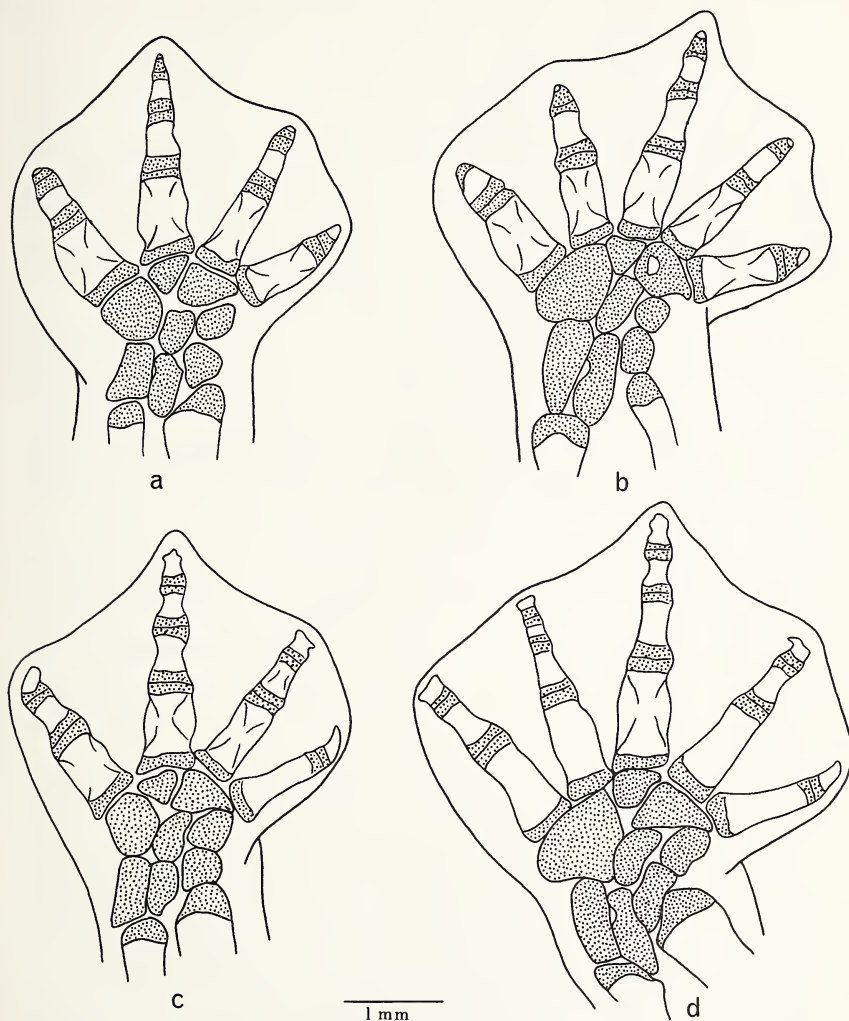


FIGURE 2. Outlines of hands and feet of species of *Bolitoglossa* drawn from cleared and stained specimens through use of microprojector. a. Right hand of *B. ramosi* (LACM 64603). b. Right foot of *B. ramosi* (LACM 64603). c. Right hand of *B. medemi* (LACM 72067). d. Right foot of *B. medemi* (LACM 72067).

uniformly colored a deep, leaden black. The dorsal surfaces of the head, tail, and legs are similarly colored. Small, indistinct guanophores are scattered on the snout, eyelids, and around the insertion of the limbs. Ventral surfaces are distinctly lighter than dorsal ones, and have a general grayish cast. Scattered guanophores are conspicuous on the throat and anterior part of the venter. Posteriorly and on the tail small to moderately sized, irregularly shaped patches of golden cream to grayish silver pigment occur. The ground color of the tail is darker than that of the throat and belly. Ventral surfaces of the limbs are mottled black and light gray, and the hands and feet are medium gray. The iris is golden with melanic mottling.

Variation.—Specimens from the Departamento de Chocó have somewhat lighter venters with fewer light patches than the animals from the Depto. Antioquia. The Panamanian individuals are similar in coloration to the holotype, but lack light ventral patches and have indistinct guanophores. The distinction between the dark dorsal and lateral and lighter ventral coloration is somewhat sharper than in the Colombian specimens.

A total of ten adult specimens are available, nine of which are from Colombia. The single adult from Panamá will be discussed separately. Males have small, well-defined, rounded mental hedonic glands. Females are larger (4 females, 34.2–48.2, mean 42.7 mm SL; 5 males 33.7–46.7 mean 40.4 mm SL) and have longer legs (SL 3.5–4.3, mean 3.9 times hind limb length in females versus 3.4–4.0, mean 3.7 in males) than males. Limb interval is zero to 1.5 in males and one to 1.5 in females. Males have premaxillary teeth which penetrate the upper lip, but females lack them.

The single adult female from Panamá differs from the Colombian females in having premaxillary teeth. It is about the same size as the Colombian specimens but has a narrower head (SL 6.4 times head width) than any Colombian individuals (SL 5.6–6.1, mean 5.8, times head width). The feet of the Panamanian adult are somewhat narrower than those of the Colombian specimens.

The juveniles are uniformly dark dorsally and lighter ventrally, with no distinctive markings.

Osteology.—Information concerning osteology has been derived from one cleared and stained female and from stereoscopic radiographs of all adults available.

The heavily ossified, well sutured skull is as well developed as that of any member of the genus. The premaxilla bone has a dental part that is well developed. It is closely aligned with the maxillae on either side. This alignment is typical of female *Bolitoglossa*. However, the toothless condition of the relatively large premaxilla is unusual. Frontal processes of the premaxilla are stout. They ascend along the margins of the cartilaginous nasal capsule, then proceed posteriorly. Near their tips they are dilated and in close apposition. As a result, the internasal fontanelle is very small and is restricted to the anterior end of the snout. The ascending part of each frontal process bears a winglike, flattened process lying against the anteromedial surface of the car-

tilaginous nasal capsule. These processes meet similar enveloping processes of the nasal. Posteriorly the frontal processes broadly overlap the expanded anterior part of the frontals in a firm articulation. The processes fall short of the ends of the nasals, but extend beyond the anterior margin of the orbits. Nasal bones are very large and protuberant. They extend far anteriorly where they overlie the enlarged nasal capsules. The area occupied by the nasal and prefrontal of more primitive species of the genus is included within the area of the nasal. Medially and anteriorly the nasals overlap the middle parts of the frontal processes of the premaxilla. The overlapping pieces are in medial contact for a short distance, an unusual arrangement in this genus. Posteriorly the nasals overlap the frontals and terminate in rounded borders beyond the margin of the orbits, approximately at the level of the eyes. Large ventrolateral lobes of the nasals overlap the anterior margin of the relatively large facial processes of the maxillae. The nasal is evacuated posterior and medial to these lobes. The nasolacrimal duct extends from the nasal capsule through this evacuated area, then posteriorly through the lower layers of the skin to the anterior corner of the eye. The route of the duct is free of bone. This bone-free area extends from the anterior end of the evacuation in the nasals, between the nasals and the maxillae to the eyes. The maxillae are well-developed bones that extend posteriorly to the limit of the eyes. Anteriorly the maxillae are produced into a flattened sheet of bone which partially underlies and envelops the cartilaginous nasal capsule. The palatal processes are small, but the facial processes are moderately large and relatively high.

Vomers are well developed and completely separated from each other, except posteriorly where the toothed portions are in slight contact. The intervomerine fontanelle is broad. Preorbital processes extend beyond the lateral margins of the vomerine bodies. Vomerine teeth are in patches which barely extend onto the preorbital processes.

Frontals are large and stout, with a strong sutural joint along the midline. The facial portions are stout, but are not especially large, in contrast to more northern species (Wake and Brame, 1969). No marked lobes are present posteriorly, where the margin is irregular. Parietals are well developed and have the parietal spurs that are characteristic of the genus. The occipito-otic bones bear low crests over the anterior vertical and lateral horizontal semicircular canals. The ridges over the latter form braces for the relatively well-developed, vertically oriented squamosals. The large parasphenoid is very narrow anteriorly. The anterior terminus is blunt, rather than pointed. Where the parasphenoid is narrowest, the orbitosphenoids nearly contact each other on the midline. Posterior vomerine teeth are in large patches on the parasphenoid. They narrowly fail to come into medial contact. The right patch bears 91 and the left, 96 ankylosed, bicuspid teeth, in the single cleared individual. The operculum has no stilus. Quadrates are stout. They are connected to the skull by the cartilaginous parts of the suspensorium, and by the relatively large squamosals. The squamosals are very attenuated dorsally where

they fit into a depression in the wall of the otic capsule, and they are broadly expanded where they overlap the quadrates.

The hyobranchial apparatus is typical of other members of the genus (Wake, 1966).

Vertebrae are similar to those of other species of *Bolitoglossa*. The centra are spool-shaped, the intervertebral cartilages are unmineralized, and no articular condyles are formed. There are one cervical, fourteen trunk, one sacral, two caudosacral, and 26 caudal vertebrae in the cleared individual. Caudal vertebrae in other specimens number 25 (LACM 42276, 42279, both adults), 24 (LACM 42278, adult, last 5 regenerated), 22 (LACM 42277, juvenile), 19 (LACM 42280, all regenerated; KU 116534, juvenile), and 17 (KU 116537, all regenerated).

The first caudal vertebra is shorter than the next eleven vertebrae, but is the same length as the second caudosacral. All but the last two trunk vertebrae are longer than the longest caudal vertebrae (two to six), but caudal vertebrae two to ten are longer than the sacral and caudosacral vertebrae. Ribs are present on all but the last trunk vertebrae. One specimen (LACM 42279) has a small rib on one side of the last trunk vertebra. Transverse processes are short on all but the first two or three caudal vertebrae, but they are clearly present on all but the last vertebra. Transverse processes of the first caudosacral vertebra are long and directed almost perpendicularly to the body axis. Those of the second are much shorter and are directed somewhat posteriorly. The large, stout, non-bifurcated processes of the first caudal vertebra arise from the anterior margin of the vertebra (in contrast to the more central location of the caudosacral processes). From their anterior origin the processes extend first anteriorly, then sharply in a lateral direction. They do not cross those of the more anterior vertebra. This distinctive pattern of processes on the first three postsacral vertebrae is one not seen in any related or neighboring species. Processes on succeeding vertebrae arise from anterior positions and are anteriorly directed. They progressively diminish in size posteriorly. Hypapophyseal keels are absent only on the first and last two caudal vertebrae.

Hands and feet are large and distinctive. They are characterized by relative narrowness, accentuated by the presence of inordinately long central digits. Some variation in phalangeal formulae is encountered. The usual formula is 1, 2, 3, 2 for the hands and 1, 2, 3, 3, 2 for the feet. Two adults have a foot formula of 1, 2, 3, 2, 2 on one side, and several other individuals have very small penultimate and terminal phalanges in the fourth digit. Terminal phalanges are rather well developed but are erratically shaped (Fig. 2). There are seven carpals and eight tarsals, the generalized *Bolitoglossa* numbers (Wake, 1966). The tibia bears a prominent, sharp-edged crest, but has no free spur.

Remarks.—PAS 237 (LACM 72067) was captured by Norman J. Scott on a tree leaf where it was exposed at night. Other Colombian specimens were

collected during daylight hours, exposed on the surface. KU 116530 was collected in cloud forest (Myers, 1969) where it is sympatric with *B. phalarosoma*.

Range.—The Chocó region of extreme northwestern Colombia, in the Río Atrato (Caribbean) drainage, and the Río Jaque (Pacific) drainage of extreme southeastern Panamá (Fig. 8). The species ranges from about 30 to 800 m (100 to 2624 ft) in elevation.

Bolitoglossa valleculea has been the only species known from uplands of the Cordillera Central of Colombia. A second species was collected in 1968 and 1971. We name it after Jorge Eduardo Ramos, who contributed much toward the success of the Silverstone and Brame—Newcomer trips to Colombia.

Bolitoglossa ramosi, new species

Figures 2 and 3

Holotype.—LACM 64601, an adult male from near Represa de Santa Rita (= Santa Rita Dam Site), Departamento de Antioquia, Colombia. This site is between Guatapé and San Rafael at about 75° 7' W, 6° 17' N, ca. 16 km by road NE of Guatapé. The specimen was collected by Brame and Jorge E. Ramos from the rolled-up base of a large palm frond on the ground of a forested hill near the dam construction site, April 3, 1971. Elevation about 1930 m (6330 ft).

Paratypes.—LACM 64600, 64602-03, same data as holotype; LACM 42287-90, collected from bromeliads at the same locality by Philip A. Silverstone and Jorge E. Ramos, June 9, 1968.

Diagnosis.—A moderately small species (5 adult males: 37.1–45.4, mean 40.4 mm SL; 2 adult females: 37.2–46.7, mean 42.0 mm SL) with relatively high numbers of maxillary (mean 47) and vomerine (mean 32) teeth; distinguished from *B. medemi* by its greater numbers of maxillary teeth and lighter dorsal ground color; from *B. equatoriana* and *B. walkeri* by its broader head and more numerous teeth. *B. ramosi* is distinguished from other Panamanian and South American salamanders by the combination of its extensively webbed hands and feet with the third digits long and pointed, its broad head, and distinctive coloration (rich rusty red to medium gray-black dorsally, with a darker venter, and a sprinkling of orange-red color on the dorsum and bright yellow patches on the venter).

Description of Holotype.—Adult male with moderately long, truncate snout and small nostrils. Large mental hedonic gland present (2.9 mm long and 3.3 mm wide). Labial protuberances of nasolabial grooves large and well developed, extending beyond margins of jaw. Moderately long canthus rostralis gently arched. Head moderately broad (SL 6.4 times head width) and moderately long (SL 4.5 times snout-gular fold length). Deep groove below

eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Large eyes slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 1.8 mm; proceeds sharply in ventral direction at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 3.3 mm anterior to well-defined gular fold. Vomerine teeth number 26, arranged in single rows that become patched laterally. Patches extend slightly beyond lateral margins of internal nares; then row forms gentle arch to center of palate, where it is directed posteriorly. Small maxillary teeth number 55; extending posteriorly

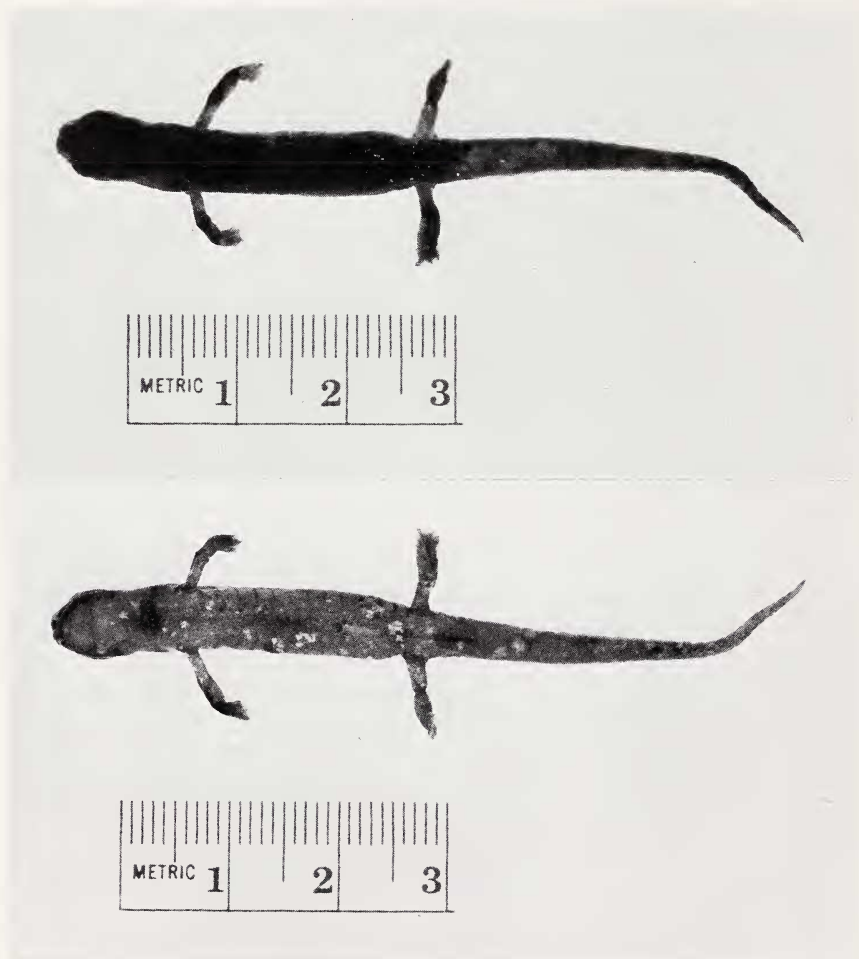


FIGURE 3. Dorsal and ventral views of paratype of *Bolitoglossa ramosi* (LACM 42289).

to point about three-fourths through eye. Premaxillary teeth (2) well anterior to projected curvature of maxillary tooth row; piercing lip. Moderately long tail (0.94 times SL) with strong lateral compression, moderately constricted at base. No postiliac glands evident. Limbs moderately long (limb interval one); SL 4.2 times right forelimb and hind limb, and 9.7 times right foot width. Webbing of hands and feet nearly complete, but tips of longer digits pointed, extending beyond limits of relatively thick web. Third digit unusually long and pointed. Hands and feet moderate in size. No subterminal pads. Fingers, in order of decreasing length, are 3, 2, 4, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 7.1; snout to gular fold (head length), 11.2; head depth at posterior angle of jaw, 3.8; eyelid length, 2.8; eyelid width, 1.8; anterior rim of orbit to snout, 3.2; horizontal orbital diameter, 2.1; interorbital distance, 2.3; distance between vomerine teeth and parasphenoid tooth patch, 0.6; snout to forelimb, 13.8; distance separating external nares, 2.8; distance separating internal nares, 1.8; snout projection beyond mandible, 1.2; snout to posterior angle of vent (SL), 45.4; snout to anterior angle of vent, 41.2; axilla to groin, 24.2; tail length, 42.8; tail width at base, 3.2; tail depth at base, 3.7; forelimb length, 10.8; hind limb length, 10.8; width of right hand, 3.7; width of right foot, 4.7.

Coloration of Holotype (in life).—This is a brightly colored salamander with a rich rusty red dorsal color on head, trunk and tail. A few dark black spots of ground color show through in some areas (especially on the snout). The venter is a dark gray-black. Ventral surfaces of the throat, trunk, and tail have widely scattered, irregularly shaped small spots and patches. These are bright pale yellow. The head is mottled rusty red and black except for the white-tipped nasolabial protuberances. The borders of the mouth are darkened. Dorsal surfaces of the upper arm and leg are light red, but lower parts of the limbs and the entire ventral side match the respective surfaces of the trunk. Dorsal and ventral surfaces of the webbed pad are relatively dark, and the phalanges tend to be outlined by some darker pigment dorsally. The eyes are dark, with heavy concentrations of melanin.

Variation.—Pertinent data are presented in Table 1. The males have longer snouts than the females. No hedonic glands are evident on the two small males but they are large and prominent on the three large ones. The largest male (the holotype) and the three largest male paratypes have premaxillary teeth which protrude from the lip. One of the small males and also LACM 64603 differ in coloration from the remaining paratypes and the holotype in having a pair of broad, white stripes extending from the tips of the nasolabial protuberances to the eyelids. The paratypes (except LACM 64603) differ from the holotype in having a lighter gray dorsal color and light orange-red patches about the base and first one-third of the tail, and also by having larger pale yellow patches ventrally.

TABLE I. Measurements and data for specimens of new species of *Bolitoglossa*

	Sex	Snout-Vent Length	Axilla-Groin Length	Head Width	Hind Limb Length	Forelimb Length	Tail Length	Numbers of Maxillary Teeth	Numbers of Vomerine Teeth	Limb Interval	Foot Width
<i>B. silverstonei</i>											
LACM 42283 ^a	♂	49.3	27.0	7.8	10.8	10.6	55.7	51	24	3	5.3
<i>B. medemi</i>											
LACM 70565	♂	46.7	24.5	8.1	12.5	12.5	47.5	59	34	0.5	5.3
LACM 42278	♂	41.7	21.4	7.4	12.4	12.0	34.6 ^b	43	22	0	4.3
LACM 42280	♂	41.3	21.6	6.9	10.6	10.6	17.8 ^b	33	32	0.5	3.7
LACM 70567	♂	38.5	20.1	6.3	9.6	9.2	36.2	35	27	1.5	3.9
LACM 42279	♂	33.7	16.7	6.0	9.3	9.4	33.2	41	29	0.5	3.3
LACM 42276 ^a	♀	48.2	26.6	8.3	12.2	12.2	36.3	41	23	1	4.8
LACM 72067 ^c	♀	47.3	26.0	7.9	11.2	11.3	36.5	50	26	1	4.8
KU 116533	♀	47.0	26.3	7.3	12.0	11.8	16.1 ^b	38	50	1.5	4.4
LACM 70568	♀	39.7	19.7	7.0	11.4	10.2	32.3	45	42	1	4.1
LACM 70566	♀	34.2	17.8	6.1	8.9	8.0	28.7	28	27	1	3.3
LACM 42277	juv.	30.0	14.1	5.3	7.3	7.1	20.6	14	20	0.5	2.7
KU 116530	juv.	28.9	16.1	5.5	7.1	7.0	7.0 ^b	23	28	1	2.7
<i>B. ramosi</i>											
LACM 64601 ^a	♂	45.4	24.2	7.1	10.8	10.8	42.8	55	26	1	4.7
LACM 64602	♂	41.4	21.4	7.1	10.4	10.3	32.2 ^b	50	31	1.5	4.1
LACM 64603 ^c	♂	40.0	21.3	6.9	10.7	10.7	29.5 ^b	38	25	1	4.0
LACM 42290	♂	37.9	19.0	6.7	9.6	9.2	29.8	47	26	1	3.2
LACM 42289	♂	37.1	20.4	6.6	9.4	9.3	33.9	41	31	2	3.2
LACM 64600	♀	46.7	24.7	7.8	11.2	10.8	36.0	50	51	2.5	4.3
LACM 42288	♀	37.2	19.5	6.6	8.8	8.6	29.7	45	37	1.5	3.2
<i>B. walkeri</i>											
UMMZ 128833 ^a	♂	40.2	21.3	6.4	10.2	9.8	32.8 ^b	29	22	1.5	4.5
MVZ 68628	♀	41.4	23.1	6.3	9.0	8.6	19.2 ^b	33	36	2.5	3.7
MVZ 68627	♀	38.9	22.0	6.2	8.7	7.9	37.0	18	28	2.5	3.2
<i>B. equatoriana</i>											
LACM 70561	♂	42.8	22.7	7.1	10.6	10.0	35.8	23	18	2	4.3
LACM 70562	♂	40.2	21.2	7.1	10.7	10.4	33.6	26	24	1.5	4.2
LACM 70550 ^a	♀	57.9	32.8	9.1	13.2	13.2	49.6	48	11	3	5.7
UIMNH 54296	♀	45.9	24.4	7.4	11.2	10.2	41.0	27	28	2	4.2
UIMNH 86692	♀	44.0	23.0	7.0	10.6	10.5	35.2	27	26	2	4.1
KU 98951	♀	43.0	22.8	7.5	10.6	10.1	____ ^b	23	24	2	4.3
LACM 70552	♀	42.6	23.5	6.7	10.1	9.7	16.3 ^b	24	18	3	3.8
LACM 70551	♀	42.4	23.1	7.0	10.3	10.0	34.9	27	21	2	4.0
UIMNH 86694	♀	41.4	22.1	6.7	9.8	9.8	28.7 ^b	19	24	2	3.9
LACM 70553	♀	40.3	20.9	6.8	9.4	9.6	33.7	20	19	3	3.9
LACM 70555	♀	39.7	21.8	6.4	9.1	8.9	35.0	27	23	3	3.6
LACM 70556	♀	39.3	21.2	6.7	9.7	9.0	29.9	14	21	1.5	4.0
LACM 70554	♀	39.0	21.7	6.6	10.1	9.9	29.0	24	17	2.5	3.6
UIMNH 86696	♀	38.3	20.6	6.2	9.2	9.1	22.1 ^b	23	20	2	3.9
LACM 70557	♀	37.5	21.2	6.3	9.0	8.8	28.2	22	17	3	3.4
LACM 70558	♀	36.8	19.7	6.1	8.9	9.0	29.3	19	17	2.5	3.5
UIMNH 86695	♀	36.5	19.3	6.3	8.7	8.6	29.2	27	23	2	4.0
LACM 70559	juv.	34.0	18.9	6.2	8.6	8.3	28.3	18	16	2	3.3
LACM 70560	juv.	32.4	16.7	5.9	7.9	7.3	25.0	4	16	2	3.0

^aholotype; ^bregenerated tails or tails missing; ^ccleared and stained.

Osteology.—Information has been derived from one cleared and stained adult male (LACM 64603) and from stereoscopic radiographs of all adults available.

The skull is well formed and bones in the posterior portion are closely sutured. The snout is short and anterior cranial elements are small, with slight or no articulations. In comparison with *B. medemi* the snout region is poorly developed. The premaxilla is small and slender, with short, distally expanded frontal processes. The processes are well separated for their entire length, but the internasal fontanelle is very small. The irregularly expanded terminal parts of the processes are small and barely overlap the anterior ends of the frontals. Lateral parts of the frontals extend anteriorly so that the tips of the processes lie more or less enclosed by the frontals. The processes extend beyond both the anterior border of the orbit and the posterior margin of the nasals. Nasal bones are of moderate size and, relative to the premaxilla, they are strongly protuberant. Their only articulation is by means of a ventrolateral lobe which barely contacts the facial process of the maxilla. The pointed posterior tips of the nasal bones extend to the anterior border of the orbits. The separation between the nasals is great, approximating their length. The posterolateral margins of the nasals and the anterodorsal margins of the facial process of the maxilla are evacuated for the passage of the nasolacrimal duct. Prefrontal bones are very erratic in shape, and they are very small. In the one cleared specimen the prefrontal of one side is an elongate bone with about one-quarter the area of the facial process of the maxilla and less than one-tenth the area of the nasal. On the other side the bone is reduced to a tiny dot that is less than one-tenth the size of its pair. Prefrontals have no contacts with other bones in this species. The maxillae extend about three-quarters through the eye. They are very slender, with well developed facial processes. The anterior ends of the maxillae are flattened, terminating in narrowed points. Palatal processes are poorly developed.

Vomers are of moderate size and are completely separated from each other. The toothed portions are drawn into processes medially, where they converge, but remain well separated. The intervomerine fontanelle is very large. Preorbital processes extend beyond the lateral margins of the vomerine bodies. Vomerine teeth are in a single row that extends beyond the lateral margin of the internal nares.

Frontals are large and well sutured to each other. Facial portions are relatively smaller than *B. medemi*. Posteriorly the bones are well sutured to the parietals. There are slight lateral lobes on the posterior margins of the frontals. Parietals are well developed and closely articulated with each other. There are no crests on the occipito-otics. The nearly vertical squamosals rest in depressions in ridges on the lateral margins of the occipito-otics. The large parasphenoid has a rather narrow, blunt-tipped anterior end. The orbitosphenoids are well separated at their ventral margins. Posterior vomerine tooth patches are not in contact medially. The right patch bears 74 and the left, 82

ankylosed, bicuspid teeth in the cleared specimen. The operculum has no stilus. Quadrates and squamosals are moderately developed.

There are one cervical, fourteen trunk, one sacral, two caudosacral and 28 (LACM 42289, 42290, 64601), 27 (LACM 64600), 25 (LACM 42288), 23 (LACM 6460, tip regenerated), or 19 (LACM 42287, juvenile) caudal vertebrae; the tail of LACM 64603 is regenerated beyond caudal vertebra seventeen. Ribs are present on all but the last trunk vertebra. The transverse processes on the first caudosacral vertebra are very long and are oriented nearly perpendicularly to the body axis. Those of the second caudosacral vertebra are shorter and extend sharply in an anterior direction. The very long, unbranched processes of the first caudal vertebra are slanted anteriorly. The slant is sharper than on the preceding vertebra. Their tips extend nearly to a level equivalent to the anterior end of the second caudosacral vertebra. The processes of these adjacent vertebrae do not overlap. Processes on the second caudal vertebra are much smaller than those on the first, and they become progressively smaller on the remaining vertebrae. The last vertebra to have distinct processes varies from the eighth to the eighteenth. The last caudosacral and first caudal vertebrae are shorter than neighboring vertebrae. Vertebrae in the anterior one-half of the tail are as long as any but the first three trunk vertebrae. The fourteenth caudal is the first vertebra that is shorter than the first caudal.

The tibia has a distinct crest but no spur. Phalangeal formulae are 1, 2, 3, 2 (or 1), and 1, 2, 3, 3 (or 2), 2 (or 1). The more distal phalanges are poorly developed, but there is a tendency for reduction and loss (Fig. 2). Terminal phalanges are extremely small and poorly ossified, with erratic shapes. Penultimate phalanges are reduced in the longer toes. Proximal phalanges are short and stout, often as broad as long. They are somewhat flattened. The distance between bony areas of a given digit is great, and often the cartilage between elements is longer than the adjacent bones. Metatarsals and metacarpals are flattened, with lateral bony webs. The outermost metapodials have characteristic shapes resulting from a large, rounded web along the margin of the bones. There are seven carpals and seven or eight tarsals. In one tarsus, D 4-5 is fused with D 3, and D 1-2 is partly mineralized in several tarsi (Fig. 2).

Remarks.—All specimens were collected either in bromeliads located within a few feet of the surface, or in the rolled bases of palm fronds on the surface of a forested hill. In 1968 the specimens were collected in sympatry with *Bolitoglossa valleculea*, a species that is widespread in the northern part of the Cordillera Central of Colombia (Brame and Wake, 1963). No *B. valleculea* were found associated with *B. ramosi* during the 1971 visit.

Range.—Known only from the type locality in the Cordillera Central of Colombia (Fig. 8).

The following most distinctive of the new species is named in honor of

Philip A. Silverstone, in appreciation of his assistance to us and in recognition of his important contributions to Neotropical herpetology.

Bolitoglossa silverstonei, new species

Figures 4 and 5

Holotype.—LACM 42283, an adult male from Quebrada Bochoramá, Loma de Encarnación, Departamento de Chocó, Colombia, about 51 km (32 mi) SE Quibdo at approximately 76° 23' W, 5° 20' N. This site is a "one-hour walk" SE Playa de Oro. The specimen was collected in a rolled plantain leaf on a steep hillside near a stream at about 400 m (1312 ft) elevation by Philip A. Silverstone and Jorge E. Ramos on May 31, 1968. The species is known only from the holotype.

Diagnosis.—A moderate-sized species (49.3 mm SL) with moderate numbers of maxillary (51) and vomerine (24) teeth; distinguished from *B. biseriata* by its larger feet and more numerous maxillary teeth; from *B. sima* by its shorter legs and more numerous maxillary teeth. *Bolitoglossa silverstonei* is distinguished from other Panamanian and South American species by the combination of its extensively webbed hands and feet, distinctive ventral coloration (cream with a light peppering of small brownish spots), and size and dentitional features.

Description of Holotype.—Adult male with moderately long, somewhat truncate snout and small (2.0 mm wide), nearly circular mental gland and small nostrils. Labial protuberances of nasolabial grooves moderately large, extending below lower jaw margin. Head moderately broad (SL 6.4 times head width) and long (SL 4.3 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Eyes moderately small, slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 2.2 mm, then sharply ventrad at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 4.2 mm anterior to sharply defined gular fold. Vomerine teeth number 24, in moderately patchy rows that extend slightly beyond lateral borders of internal nares. From lateral terminus, rows extend medially in nearly straight line to near center of palate, then bend sharply posteriad and closely approach (1.0 mm separation) parasphenoid tooth patch. Small maxillary teeth number 51; extending posteriorly to point about three-fourths through eye. Large premaxillary teeth (two) pierce lip. Long tail (1.1 times SL) rounded and moderately constricted at base. Postiliac glands indistinct. Limbs moderately short (limb interval three). Standard length 4.6 times right forelimb, 4.5 times right hind limb, and 9.3 times width of right foot. Webbing of hands and feet extensive, nearly complete, with only tips of longer digits extending slightly beyond web (Fig. 5). No subterminal pads present. Fingers, in order

of decreasing length, are 3, 2, 4, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 7.8; snout to gular fold (head length), 11.5; head depth at posterior angle of jaw, 4.8; eyelid length, 3.2; eyelid width, 2.0; anterior rim of orbit to snout, 3.8; horizontal orbital diameter, 2.7; interorbital distance, 3.3; distance between vomerine teeth and parasphenoid tooth patch, 1.0; snout to forelimb, 14.5; distance separating internal nares, 2.4; distance separating external nares, 3.0; snout projection beyond mandible, 0.9; snout to posterior angle of vent (SL), 49.3; snout to anterior angle of vent, 45.1; axilla to groin, 27.0; tail length, 55.7; tail width at base, 3.9; tail depth at base, 3.9; forelimb length, 10.6; hind limb length, 10.8; width of right hand, 4.1; width of right foot, 5.3.

Coloration of Holotype (in alcohol).—This is a rather light-colored salamander. A reddish brown dorsal mottling overlies the blackish purple ground color. The dorsal pigmentation is distinctly darker than that of the ventral surfaces. Lateral surfaces of the trunk and tail are light reddish brown with some scattered melanophores. An indistinct ventrolateral stripe of blackish purple sharply separates the dark dorsal and lateral from the light ventral pigmentation. The broad stripe of the trunk becomes narrow and discontinuous on the tail. All ventral surfaces are light golden cream to grayish white, peppered with minute, widely scattered melanophores that are clearly visible over the entire surface. Some coalescence of melanophores occurs laterally, producing larger spots of pigment. The head is colored like the trunk, dark dorsally and light ventrally. The whitish ventral coloration of the throat extends along the upper lip region and in front of the eyes. The small eyes have a reddish brown iris, with a gold ring surrounding the horizontally elliptical pupil. Limbs are dark dorsally and light ventrally, with other markings similar to the respective parts of the trunk. The hands and feet are light dorsally and ventrally, and there are no obvious ventral melanophores.

Osteology.—Stereoscopic radiographs have provided all of the following information. The skull is comprised of well-articulated bones and is generally well developed. The premaxilla has a very small dental process which is placed well ahead of the maxillae. Frontal processes of the premaxilla are separated for their entire lengths. The processes are large and expanded near their tips. Nasal bones are large and strongly protuberant. No prefrontal bones can be seen. Vomers are well separated on the midline. The preorbital processes of the vomers extend laterally well beyond the limits of the internal nares. No stilus is present on the middle ear bone. Ribs are present on all but the last trunk vertebra. There are one cervical, fourteen trunk, one sacral, two caudosacral, and 38 caudal vertebrae. The transverse processes on the first caudosacral vertebra are very long and slant posteriorly. Those on the second caudosacral vertebra are much shorter and slant slightly in an anterior direction. The long, unbranched processes of the first caudal vertebra arise near its anterior end and extend sharply in an anterior direction. They termi-

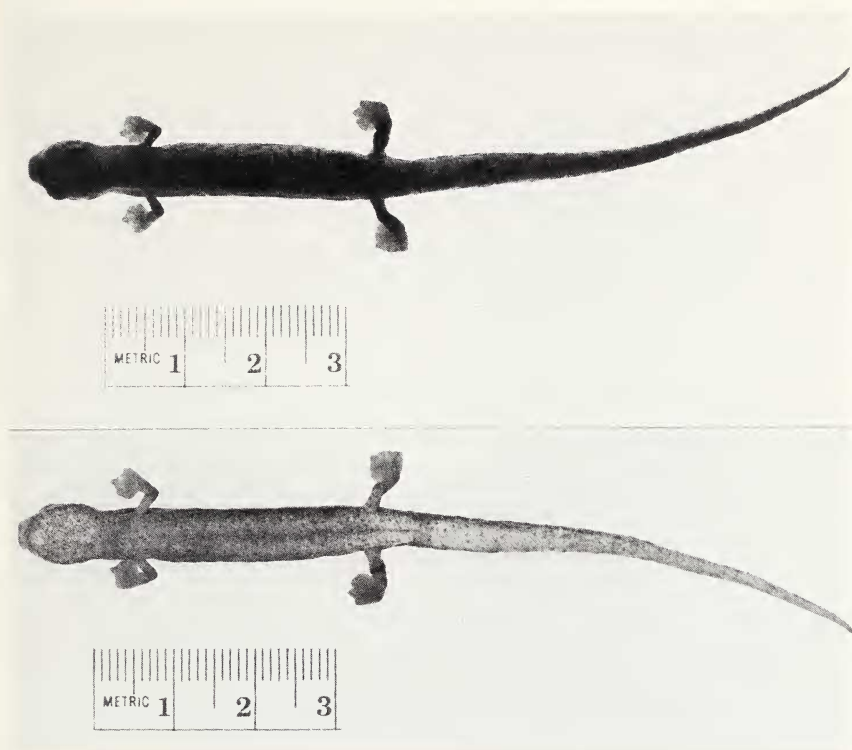


FIGURE 4. Dorsal and ventral views of paratype of *Bolitoglossa silverstonei* (LACM 42283).

nate beyond the point of attachment of the processes of the second caudosacral vertebra. The tips of the processes of the last caudosacral and first caudal vertebrae do not cross. Transverse processes of the remaining caudal vertebrae are progressively smaller. All are located near the anterior end of the vertebrae and are oriented sharply forward. They are discrete on the first 30 vertebrae. As is usual in species with constricted tail bases, the last caudosacral and first caudal vertebrae are shortened, relative to neighboring vertebrae. Posterior to this region the vertebrae are longer. The fourth through seventh caudal vertebrae are as long as the longest trunk vertebrae (two and three). The first vertebra shorter than the first caudal vertebra is the seventeenth caudal. From that point the vertebrae are progressively shorter to the tail tip. No tibial spurs are present. Phalangeal formulae are 1, 2, 3, 2 and 1, 2, 3, 3, 2. All phalangeal elements are small and poorly developed, and the abrupt decrease in size from the proximal to the distal elements in the longest digits is striking (Fig. 5). Terminal phalanges are all minute and unexpanded; most are tiny points of bone. Much cartilage is present at the ends of the

metapodials and phalanges, and the distance from one bony area to another is always greater than the length of the distal bony element. Metapodials are dumbbell-shaped with only slight lateral expansion.

Remarks.—Playa de Oro is located in the Chocó forest area of Colombia, in a region identified as wet tropical forest (Holdridge System) by Espinal and Montenegro (1963). Previously only *B. biseriata* has been known from this area, but discovery of *B. silverstonei*, *B. medemi*, and *B. phalarosoma* from northwestern Colombia and from Panamá suggests that this has been a region of lowland diversification. Two additional species, *B. sima* and *B. chica*, occur in the Ecuadorian portion of the Chocó.

Range.—Known only from the type locality in the lowlands of northwestern Colombia (Fig. 8).

During the past ten years we have been generously aided in our efforts by the cooperation and encouragement of Professor Charles F. Walker of the Museum of Zoology, University of Michigan. It is a pleasure to name the following Colombian species in his honor.

Bolitoglossa walkeri, new species

Figures 5 and 6

Holotype.—UMMZ 128833, an adult male from "Television Tower Mountain," 15 km WNW Cali and 0.9 km S El Jordan, Departamento de Valle, Colombia. The specimen was collected from a bromeliad in cloud forest at an elevation of 2050 m (6724 ft) by Walter Moberly and Kraig K. Adler on July 17, 1965.

Paratypes.—MVZ 68627-28, 4 km NW San Antonio, Depto. Valle, Colombia, 1982 m (6500 ft) elevation.

Diagnosis.—An apparently small species (3 adults 38.9–41.4, mean 40.2 mm SL) with low numbers of maxillary (mean 27) and moderate numbers of vomerine (mean 28) teeth. Distinguished from *B. equatoriana* by its narrower head, less extensively webbed, slightly smaller hands and feet, and ventral coloration (dirty white to gray, with some streaks of darker pigment and an overlay of brassy pigment, but without the encroachment of dark pigment which leaves the large, whitish spots characteristic of *B. equatoriana*); from *B. medemi* by its narrower head, less extensively webbed feet, and shorter legs; from *B. ramosi* by its narrower head and less numerous teeth. *Bolitoglossa walkeri* differs from other Panamanian and South American *Bolitoglossa* by the combination of its extensively webbed hands and feet, color, and its size and dentitional features (Table 1).

Description of Holotype.—Adult male with moderately short, truncate snout and pronounced, rounded, mental hedonic gland; small nostrils. Labial protuberances of nasolabial grooves well developed, extending below lower jaw margin. Strongly arched canthus rostralis moderately long. Head mod-

erately broad (SL 6.3 times head width) and long (SL 4.4 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Eyes relatively large, moderately protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 1.8 mm, then sharply ventrad at

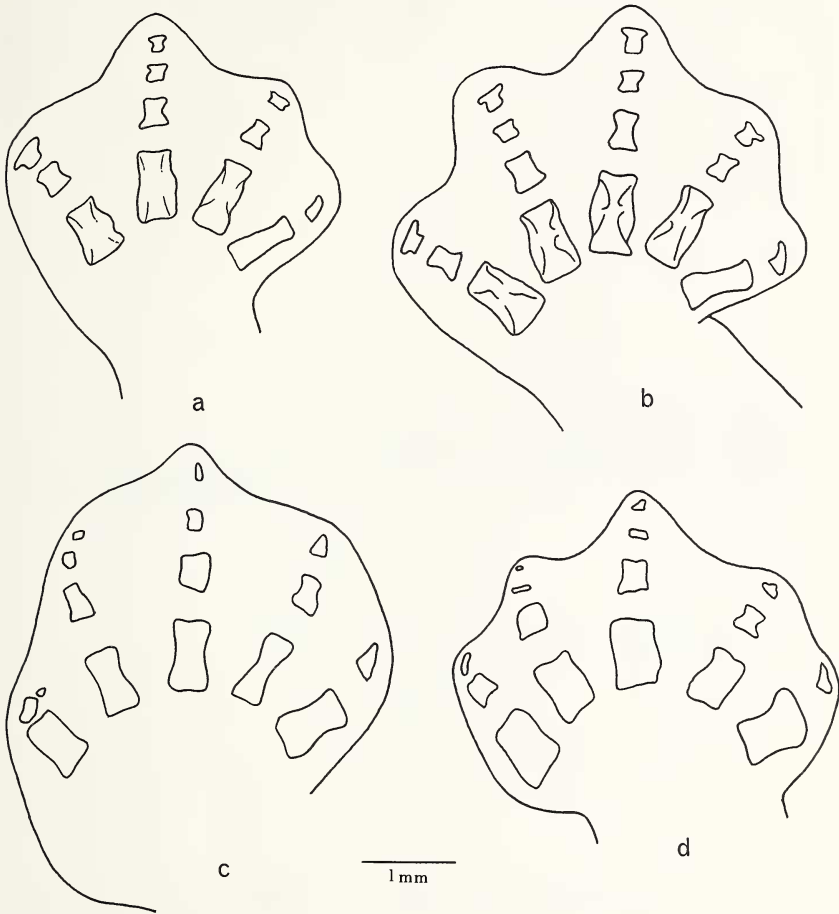


FIGURE 5. Outlines of hands and feet of three species of *Bolitoglossa*, drawn from radiographs through use of microprojector. Bony parts of digits are outlined. a. Right hand of holotype of *B. walkeri* (UMMZ 128833). b. Right foot of holotype of *B. walkeri*. c. Right foot of holotype of *B. silverstonei* (LACM 42283). The left side of the drawing is distorted as a result of fixation artifact. d. Right foot of *B. equatoriana* (KU 98951). The foot is slightly distorted on the left and slightly foreshortened as a result of fixation artifact.



FIGURE 6. Dorsal and ventral views of holotype of *Bolitoglossa walkeri* (UMMZ 128833).

level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 3.2 mm anterior to sharply defined gular fold. Vomerine teeth number 22, arranged in single rows extending from one-half to two-thirds diameter of internal nares; from lateral terminus, rows form moderately strong arches to center of palate, where two rows nearly meet. Small maxillary teeth number 29; extending posteriorly to point about one-half through eye. Single premaxillary tooth pierces lip. Relatively short tail (0.82 times SL) has slight lateral compression and is slightly constricted at base. Postiliac glands small, indistinct. Limb length moderate with limb interval of 1.5. Standard length

4.1 times right forelimb, 3.9 times right hind limb, and 9.0 times width of right foot. Webbing of hands and feet extensive, thin. Tips of all digits discernible, longer digits protruding substantially from web. Digital tips broadly rounded. Hands and feet relatively large. No subterminal pads. Fingers, in order of decreasing length, are 3, 4, 2, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 6.4; snout to gular fold (head length), 9.2; head depth at posterior angle of jaw, 3.6; eyelid length, 3.2; eyelid width, 1.8; anterior rim of orbit to snout, 3.0; horizontal orbital diameter, 2.3; interorbital distance, 2.8; distance between vomerine and parasphenoid teeth, 0.5; snout to forelimb, 11.8; distance separating internal nares, 2.0; distance separating external nares, 2.7; snout projection beyond mandible, 1.1; snout to anterior angle of vent, 35.8; snout to posterior angle of vent (SL), 40.2; axilla to groin, 21.3; tail length, 32.8; tail width at base, 2.8; tail depth at base, 3.2; forelimb length, 9.8; hind limb length, 10.2; width of right hand, 3.6; width of right foot, 4.5.

Coloration of Holotype.—In life (from field notes of Kraig Adler): "Golden brown above in different shades, with blackish spots and blotches. Cream white streaks running lengthwise, especially over vent and on tail; black "V's" on neck, pointing outwards; some faint reddish pigment on dorsum, especially in midline. Dark golden below, light tan golden between eye and nasolabial groove, nose region speckled with various shades of golden. Belly dirty white overlaid with much brassy pigment; some few black streaks, also at posterior end of anus [sic]; throat heavily flecked with golden, especially at anterior end; mental gland bright golden; soles of hands and feet pinkish (=blood) and golden." After several years in alcohol the brighter pigments have faded, but the pattern remains distinct. The impression is of a rather dark tannish brown animal with a much lighter venter. The whitish ventral pigment is more sharply demarcated from the lateral dark pigment of the tail than of the trunk. The mental gland is light and prominent on the relatively dark throat.

Variation.—Pertinent data are presented in Table 1. The holotype is a male and the two paratypes are females. The paratypes have proportionally shorter limbs (limb interval 2.5 rather than 1.5) and narrower feet (SL 11.2–12.2 times right foot width, rather than 9.0) than the holotype. Both features are sexually dimorphic in similar ways in most species of *Bolitoglossa*. Premaxillary teeth are absent in one paratype and fail to protrude from the lip in the other; these are also female characteristics.

One specimen, MVZ 68628, is colored like the holotype, but has a somewhat darker venter which lacks dark streaks, whereas MVZ 68627 has a lighter dorsal ground color than the holotype, but has a similar ventral coloration. This animal is briefly described in the field notes of the collector, A. H. Miller, as follows: "The light areas of the back, belly and undertail surface

were yellow or bronze in life so that the whole animal was distinctly light and bright."

Osteology.—All information has been derived from stereoscopic radiographs. The skull is well developed with well articulated bones. The small, slender premaxilla has relatively short, divergent frontal processes. The dilated tips of these processes fall short of the posterior margin of the nasals. The large, protuberant nasals have distinct lateral lobes that articulate firmly with the maxillae. No prefrontals are evident. Vomers are well separated for their entire lengths, but the toothed parts approach the midline posteriorly. Pre-orbital processes of the vomers extend well beyond the lateral margins of the internal nares and bear teeth for most of their lengths. Maxillae extend about to the posterior margin of the eyes. The operculum has no stilus. Ribs are present on all but the last trunk vertebra, but those on the next to last vertebra are very small in the holotype. There are one cervical, fourteen trunk, one sacral, two caudosacral and 28 caudal vertebrae in the single specimen that has a complete tail.

The long, stout, transverse processes on the first caudosacral vertebra are nearly perpendicular in orientation, but have a slight posterior slant. The shorter and more slender processes on the second caudosacral vertebra have a sharp anterior slant. These processes are stouter and less slanted in the holotype than in the paratypes. Their tips reach to a point about one-third through the preceding vertebra. The very long processes of the first caudal vertebra are long and sinuous. They slant strongly in an anterior direction. Tips of the processes extend beyond the bases of the processes on the second caudosacral vertebra, but the processes of the adjacent vertebrae do not overlap. The processes are not branched. Processes on succeeding vertebrae are progressively shorter. They are visible to about the nineteenth vertebra, but are minute beyond the seventh. All lie at the anterior end of the vertebrae and slant anteriorly.

The second caudosacral and first caudal vertebrae are shorter than all but the first trunk vertebra, which equals them in length, and the seventeenth and succeeding caudal vertebrae. The second through eighth caudal vertebrae are as long as the longest trunk vertebra (the seventh), and the third caudal vertebra is the longest in the entire column.

No tibial spur is present, but a small ridge is present in mid-shank on the left tibia in the holotype. Phalangeal formulae are 1, 2, 3, 2 and 1, 2, 3, 3, 2. Digits are well developed. Phalangeal elements are increasingly shortened toward the digital tip. Most are dumbbell-shaped. Terminal phalanges are expanded at their tips. Distance between the bony parts of the digits is always less than the length of the shortest phalanx of the digit. Lateral weblike processes of the metatarsals extend into the fleshy web (Fig. 5).

Remarks.—All of the specimens were collected in cloud forest at intermediate elevations. The holotype was taken from a bromeliad. Alden and Virginia Miller collected MVZ 68627 during the day (March 9, 1958) while

it was exposed on the surface of a large (five inch) leaf hanging from a flowering epiphyte that was not noticeably moist. Dr. Miller collected the other paratype (MVZ 68628) during the day (September 9, 1958) in a brushy, thick part of the forest. It was apparently dislodged from its position in the foliage, since it was found on the ground as a path was retraced. The individual had, as yet, not righted itself.

Range.—This species is known only from neighboring localities in cloud forest of intermediate elevation (about 2000 m) WNW of Cali, Depto. de Valle, Colombia (Fig. 8).

Examples of an undescribed species of salamander have been collected in sympatry with *Bolitoglossa peruviana* on several occasions. This species, named for its geographic location, is the sixth form discovered in Ecuador.

Bolitoglossa equatoriana, new species

Figures 5 and 7

Holotype.—LACM 70550, an adult female from Limón Cocha, 0° 24' S, 76° 37' W, Provincia de Napo, Ecuador. The specimen was collected at a secondary-primary growth border, 1 m above the ground, on August 5, 1971 by W. Ronald Heyer. Elevation 260 m (850 ft).

Paratypes.—LACM 70551-64 (14 specimens) collected by W. Ronald Heyer between June 11 and August 5, 1971; KU 98951, UIMNH 86692, UIMNH 86694-96 collected by different collectors between July 18 and July 28, 1965 at the type locality.

Diagnosis.—A moderate-sized species (15 females: 36.5–57.9, mean 41.7 mm SL; two males: 40.2–42.8, mean 41.5 mm SL) with low numbers of maxillary (mean 25) and moderate numbers of vomerine (mean 21) teeth. Distinguished from *B. walkeri* by its broader head, more extensively webbed and slightly longer hands and feet, and spotted ventral color pattern; from *B. medemi* by its less numerous maxillary teeth and somewhat shorter legs; from *B. ramosi* by its narrower head and less numerous maxillary teeth; from *B. peruviana* by its broader head, larger hands and feet, and less numerous maxillary teeth, as well as by its spotted ventral color pattern; and from *B. altamazonica* by its broader head, larger hands and feet, and spotted ventral color pattern. *Bolitoglossa equatoriana* is distinguished from all other Panamanian and South American species of *Bolitoglossa* by the combination of its extensively webbed hands and feet, coloration, and its size and dentitional features (Table 1).

Description of Holotype.—Adult female with moderately short, relatively broad, truncated snout. Nostrils rather small, nasolabial protuberances moderately developed. Slightly arched canthus rostralis of moderate length. Head of moderate width (SL 6.4 times head width) and length (SL 4.3 times snout-gular fold length). Deep groove below eye extends for almost full length of orbit, following curvature of eye, but does not communicate with lip. Mod-

erately large eyes only slightly protuberant. Well-defined postorbital groove extends posteriorly from eye as shallow depression for 2.8 mm; then sharply ventrad at level of posterior end of mandible and across gular area as nuchal groove, parallel to, and 5.1 mm anterior to sharply defined gular fold. Vomerine teeth number 11, arranged in single rows that extend to center or to lateral margin of internal nares. Slightly arched rows extend nearly to midline on palate, but have no posterior extension. Small maxillary teeth number 48; extending to point about one-half through eye. Three premaxillary teeth. Relatively short tail (0.86 times SL) is laterally compressed, with strong basal constriction. Postiliac glands not evident. Limbs are of moderate length (limb interval 3); SL 4.4 times right forelimb, 4.4 times right hind limb, and 10.2 times right foot width. Webbing of hands and feet extensive, moderately thick. Finger and toe tips, especially of third digits, protrude substantially from webbed pad. Tips of third fingers and toes pointed, others rounded. No subterminal pads. Hands and feet moderately large. Fingers, in order of decreasing length, are 3, 4, 2, 1; toes, in order of decreasing length, are 3, 4, 2, 5, 1.

Measurements (in mm) are as follows: Head width, 9.1; snout to gular fold (head length), 13.4; head depth at posterior angle of jaw, 4.6; eyelid length, 3.8; eyelid width, 2.0; anterior rim of orbit to snout, 3.7; horizontal orbital diameter, 2.2; interorbital distance, 3.3; distance between vomerine teeth and parasphenoid tooth patch, 0.8; snout to forelimb, 16.7; distance separating internal nares, 2.4; distance separating external nares, 3.1; snout projection beyond mandible, 1.0; snout to posterior angle of vent (SL), 57.9; snout to anterior angle of vent, 53.4; axilla to groin, 32.8; tail length, 49.6; tail width at base, 3.7; tail depth at base, 4.4; forelimb length, 13.2; hind limb length, 13.2; width of right hand, 4.2; width of right foot, 5.7.

Coloration of Holotype (in alcohol).—The dorsal color consists of a distinct though irregular beige to gray dorsal band divided down the middle by a dark blackish brown thin stripe of ground color. The ground color of the lateral surfaces is much darker than that of the dorsal and ventral surfaces. The venter appears somewhat light because of the many tiny bluish white cells covering much of the blackish ground color. The tiny spots are grouped together as patches on the last three-fourths of the tail venter. The front of the head is a medium brown and the back of the head is covered by the anterior end of the dorsal band. The hind limbs have a considerable amount of beige and gray to brown mottling dorsally, but the dorsal area of the front limbs is mostly a blackish brown ground color. The inside half of the hands and feet are covered dorsally with many tiny light colored spots overlying the ground color. The limbs all have some of these spots ventrally but the ventral surfaces of the hands and feet are an immaculate gray-black.

Variation.—Pertinent data are presented in Table 1. The female holotype is considerably larger (57.9 mm SL) than the largest paratype (45.9 mm SL). Most of the paratypes are adult females except for two males and four juve-

niles. Standard length is from 5.7 to 6.4 (mean 6.1) times head width in the entire sample. Limb length is somewhat variable in the series, and the holotype has relatively broad hands and feet (SL 10.2 times right foot width in holotype, 9.1 to 11.2, mean 10.4 in paratypes). The holotype has the third longest tail (0.86 times SL, versus 0.58 to 0.89, mean 0.79 in paratypes).

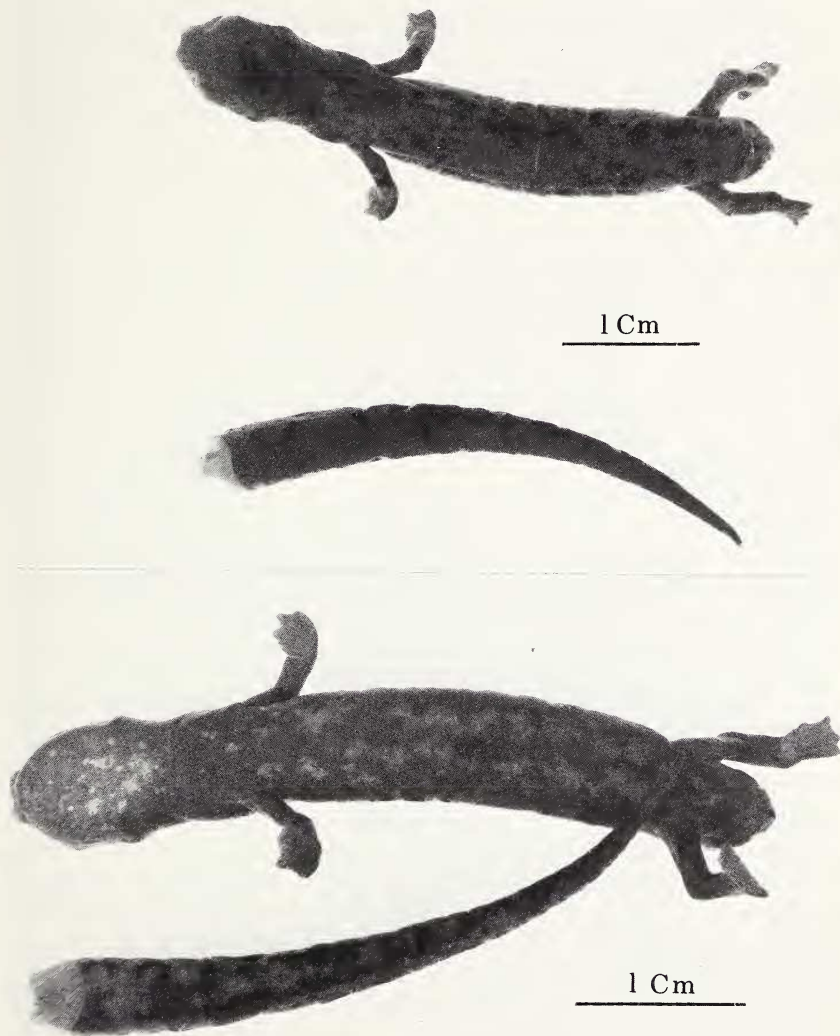


FIGURE 7. Dorsal and ventral views of a paratype of *Bolitoglossa equatoriana* (UIMNH 54296).

Digital tips of the holotype are like most of the paratypes. The tip of digit three is pointed with the other digits having more rounded tips. There is considerable variation in dorsal coloration. The holotype has a distinct though irregular beige to gray dorsal band divided by a dark blackish brown stripe of ground color down the middle; one other specimen has a uniform broad beige dorsal band; six specimens have weak or partial dorsal bands of beige to gray; two have a few dorsal light brown patches; two are uniform blackish brown dorsally. The type series varies in ventral coloration as follows: five specimens have a few to moderate numbers of mostly small, bluish silver to white spots or patches; thirteen have an irregular row of moderate-sized, bluish silver to white patches on either side of the midline (see paratype ventral view, Fig. 7); and the holotype is covered ventrally by hundreds of tiny iridophores.

Osteology.—All information has been derived from stereoscopic radiographs of the type series. The skull is well ossified and the bones are well articulated. The premaxilla is small and slender but frontal processes may be well developed. The frontal processes of UIMNH 54296 are slender and are not expanded at their tips. Those of some other specimens are expanded at their tips. The processes are separated for their entire length in all specimens. The large, protuberant nasals have a strong, extensive articulation with the maxillae. Prefrontals are definitely present in some individuals but absent in others. Vomers are well separated for their entire lengths. Preorbital processes of the vomers extend laterally well beyond the limits of the internal nares. Maxillae are of moderate size and extend about to the posterior margin of the eyeball. There is no stilus on the operculum. All but the last trunk vertebrae bear ribs. There are one cervical, fourteen trunk, one sacral, two caudosacral and from 23 to 30 caudal vertebrae in those specimens with complete tails. The long, stout transverse processes of the first caudosacral vertebra are directed nearly perpendicularly to the body axis, but with a slight posterior slant. The shorter processes on the second caudosacral vertebra slant in an anterior direction. Very long, unbranched processes are present on the first caudal vertebra, and these slant sharply toward the head. They do not cross the processes of the second caudosacral vertebra even though they extend in front of the base of the latter. Processes of succeeding vertebrae are progressively smaller. They lie at the anterior end of each vertebra and slant anteriorly. Caudal transverse processes are visible as far as the seventeenth vertebra in one adult, but they are small and highly variable in degree of development past the tenth vertebra. In the basal part of the tail the vertebrae increase in length, and the fourth and fifth caudal are as long as the longest (anterior two to six) trunk vertebrae in some, but a little shorter in others. About the thirteenth caudal is the first that is shorter than the three vertebrae immediately behind the sacrum. Vertebrae are progressively shorter from that point to the tail tip. No tibial spurs are present. Phalangeal formulae in some individuals are 1, 2, 3, 2; 1, 2, 3, 3, 2. A tendency toward phalangeal reduction is apparent and formulae may be 1, 2, 3, 1 and 1, 2, 3, 2, 1 in extreme instances. Terminal

phalanges are usually small and short, often being broader than long. They are rounded at their tips, and usually neither pointed nor expanded. Penultimate phalanges of the longest digits are small and often broader than long. Distance between the bony parts equals or surpasses the length of the penultimate phalanges in the longest digits. Terminal phalanges are shorter and smaller than penultimate ones in most instances. Metapodials are flat and broad, with some lateral bony growth extending into the fleshy web.

Remarks.—Found between 7:30 and 9:30 PM, from 0.5 to 2 m (1½ to 6½ ft) above the ground on broad leaves, palm leaves and stems, along the stream banks in secondary growth, secondary-primary border, and in agricul-

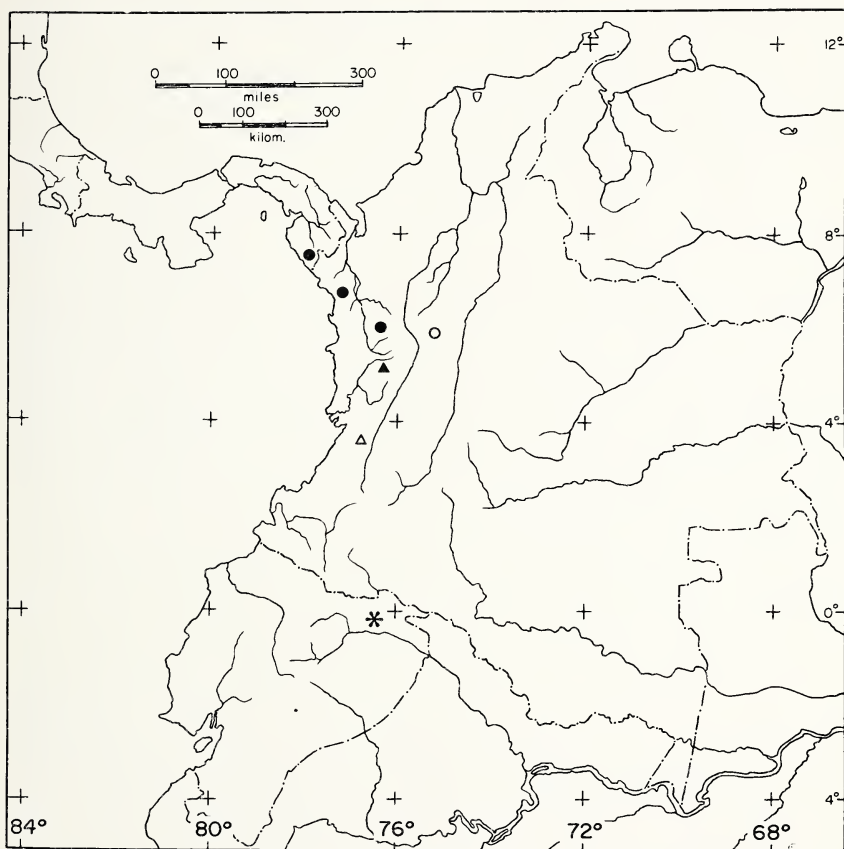


FIGURE 8. Distribution of five new species of *Bolitoglossa* in Panamá, Colombia, and Ecuador. Symbols: ● *Bolitoglossa medemi*; ○ *B. ramosi*; ▲ *B. silverstonei*; △ *B. walkeri*; * *B. equatoriana*.

tural clearings. It occurs in sympatry with the smaller and more slender *B. peruviana*.

Range.—Known only from the type locality in the Amazonian lowlands of Ecuador (Fig. 8).

DISCUSSION

In 1963 we discussed the relationships of the South American members of *Bolitoglossa*, and our views have recently been elaborated (Wake and Brame, 1966; Wake, Brame and Myers, 1970). The continued discovery of new populations and undescribed species points up the tentative nature of such discussions and the need for continuing revision. Nevertheless, it is useful to present our current views concerning species relationships, even in a developmental state, for they may aid in planning research projects and in zoogeographic work. Small samples and incomplete knowledge make full documentation impossible. However, we can present the basis for our character analysis and the kind of reasoning used.

Characters subject to interspecific variation are divided into discrete states for analytical purposes. Direction of character state change is determined in several instances. Usually this is based on out-group comparisons, with conditions that are present in more generalized relatives (such as the extratropical plethodontids) considered to be primitive. In some instances it is possible to identify one or more highly specialized states, but operationally the primitive state is identified by following the trend in specialization back to the simplest or most generalized condition by phenetic methods. Correlation of character state trends with other trends, for example, geographic patterns, is sometimes used in initial analysis. We have come to expect more ancestral states among northern and upland members of a given group, and derived states in species that are southern, lowland, or both. Finally, as a working hypothesis we expect the more derived state of a given character to be present in species in which derived states of many other characters are present. This last criterion involves some circularity in reasoning, and is used only tentatively and when other criteria are not applicable. Our knowledge of the neotropical salamanders is not sufficient to detect all of the parallelism and convergence which we suspect are present, and the fact that few characters are used in our analysis increases our chance of error. Hopefully future work will improve our ability to detect these phenomena, and will also increase the number of characters, thus diminishing the chance of error. Larger series will permit quantification and the use of continuously variable characters.

Characters:

Size.—Average adult size is small (ca. 40 mm SL), moderate (50–60 mm SL), or large (ca. 70 mm SL). Intermediate conditions (e.g., moderately small) are recognized. Moderate size is characteristic of many generalized neotropical salamanders, and is probably close to the ancestral condition.

Either extreme is considered derived, but examples of parallelism are suspected. The character has low reliability on a genus-wide basis, but may be of use within a species group established on other grounds.

Structure of Hands and Feet.—This is one of the most complex and useful sets of characters. Much information can be derived from detailed consideration of both external and internal structure of the appendages. Categories of foot-webbing have been outlined previously (Wake and Brame, 1969). The primitive hand and foot has little webbing, large and discrete digits and a full complement of phalangeal and mesopodial elements. Terminal phalanges are primitively large and well developed, and cutaneous subterminal pads are well developed. Derived characters include increase in webbing, decrease in number and size of phalangeal and mesopodial elements (through loss and fusions) and loss of digital integrity. Many types of reduction trends, all considered to be derived, are found. These include reduction in size, or loss, of the subterminal pads; reduction in size and degree of development of certain phalanges, for example, the terminals; reduction in total phalangeal bone relative to metapodial bone; disproportionate digital reduction, for example the central relative to the first digit. Also important are the shape of the toe tips, the cutaneous outline, the degree of flattening, and the proportions of limbs, feet and digits.

Numbers of Maxillary and Vomerine Teeth.—Numbers of maxillary teeth in adults are low (mean 0–30), moderate (30–60), or high (above 60). Similar categories for vomerine teeth in adults are low (0–20), moderate (20–30), and high (above 30). Moderate numbers characterize generalized relatives and are considered ancestral; both extremes are derived. Teeth increase in number with increasing size, but at different rates in different species. The values given here are not absolutes, but must be considered relative to size of the species. Thus the number of teeth in adults of a small species may be considered to be high, while the same number for a large species might be considered moderate or even low. Eventually we hope to deal with such ontogenetically variable characters in a more satisfactory manner.

Head Width.—Heads are narrow (greater than 6.7 times SL), moderate (6.3–6.6), or broad (less than 6.3). The character must be used with caution, since the proportion changes with age and size, to a degree. Moderate heads are closest to the ancestral condition and either extreme is considered to be derived.

Coloration.—We are unable to break the color continuum into discrete states. Nevertheless, certain features, such as unusual pigmentation, bands, stripes, spotting and streaking patterns, etc., are frequently used when comparing species within groups.

Behavioral Attributes.—Terrestrial habits are considered to be primitive for *Bolitoglossa*. Arboreal habits, varying from a tendency toward arboreality to complete arboreality, are considered to be derived.

Comparative Osteology.—Large numbers of osteological features have

potential value in systematic work (see Wake, 1966), but unfortunately the small samples available for most South American species preclude extensive use of such characters. In general, any reduction, fusion, loss or elaboration of the presumed ancestral condition is considered derived. Osteological features that are used for these species include presence or absence of prefrontal bones and tibial spurs, shape of the nasals, premaxillae, maxillae, and vomers, and arrangement of the transverse processes of the caudosacral and caudal vertebrae. Features associated with the hands and feet have been discussed above.

Certain other characters are used within species groups for the purposes of comparing close relatives in some detail. These include some relatively subjective features, such as snout shape and degree of protuberance of the eyes, as well as proportional relationships, such as relative leg, tail, and head lengths.

Most characters have been used in a phenetic manner, and those species which have high similarity are considered to be more closely related than those with low similarity. All of the following groups have been recognized on the basis of total similarity, with group borders recognized by discontinuities. In a fluid situation, such as obtains in the genus *Bolitoglossa* in South America, undescribed species might easily fill one of these discontinuities, necessitating changes in this arrangement in the future. Within the species groups, attention is focused on direction of change in characters, and relative degree of derivation of the various species. Attention is also given to the degree of derivation of one group relative to others.

The genus *Bolitoglossa* is by far the largest in the Order Caudata, with over 60 species. It is convenient to recognize informal species groups, which in turn form major assemblages. The species groups are not of equivalent rank, but are comprised of from one to many species. Most have discrete geographic patterns, and close relatives are not usually sympatric. Many of the species groups appear to have resulted from the fragmentation and diversification of what once were more or less continuously distributed populations. This pattern is apparent in the *helmrichi* group of Nuclear Central America (Wake and Brame, 1969) and in the *adspersa* group of northern South America (Brame and Wake, 1963; Wake, Brame and Myers, 1970). Because of our fragmentary knowledge of South American species we defer characterization of these groups to a later date.

The following species groups and subgroups occur in South America and adjacent Panamá:

- A. The *adspersa* group (subgroup 1. *hypacra*, *adspersa*, *vallecula*, *savagei*, *taylori*, *borburata*, *orestes*; subgroup 2. *palmata*; subgroup 3. *nicefori*, *capitana*, *pandi*).
- B. The *sima* group (*sima*, *chica*, *biseriata*, *silverstonei*).
- C. The *medemi* group (*medemi*, *ramosi*, *walkeri*, *equatoriana*).

D. The *altamazonica* group (*altamazonica*, *peruviana*).

E. The *phalarosoma* group (*phalarosoma*).

The major departures from our arrangement of 1963 are: 1) the description of *B. taylori* and its addition to the *adspersa* group; 2) the dissolution of the *palmata* group and the assignment of *B. orestes* and *B. palmata* to different subgroups of the *adspersa* group; 3) the division of the *altamazonica* group and the uniting of the coastal species (*B. sima*, *B. chica*) with *B. biseriata*, formerly of the *adspersa* group, to form the *sima* group; 4) the description of *B. silverstonei* as a member of the *sima* group; 5) the description of *B. ramosi*, *B. medemi*, *B. walkeri*, and *B. equatoriana*, members of the *medemi* group.

The major division is between the relatively primitive *adspersa* group and the other, more derived groups. The *sima* and *altamazonica* groups share numerous derived features in proportions and foot structure, all perhaps related to lowland, arboreal existence. They are separated by coloration and osteological differences. The *medemi* group is more similar to these two groups than to any other, although it also has some similarity in coloration, proportions and foot structure to *B. phalarosoma*. The *medemi* group is the only one of the four derived groups that contains some relatively primitive, upland species. These species have slight similarities to members of the *adspersa* group, but such species as *B. biseriata* also are similar to members of the *adspersa* group in some features. The *adspersa* group contains the most generalized South American species (*B. hypacra*, *B. valleculea*, *B. adspersa*) which resemble highland Middle American species (*B. marmorea*, *B. cerroensis*) in many features, mostly primitive states. The *adspersa* group contains several highly derived species, both in the lowlands (*B. borburata*, *B. capitana*) and the highlands (*B. orestes*, *B. palmata*).

The revised organizational scheme for South American species presented here is based in large part on our expanded knowledge of many species as the result of recent collection. Since our last survey of South American salamanders we have seen, in addition to specimens already reported, good series of specimens that were living, preserved, or both, of the following species: *B. altamazonica*, *B. peruviana*, *B. sima*, *B. chica*, *B. valleculea*, *B. adspersa*, *B. orestes*, *B. savagei*, and *B. biseriata*. Additionally we have seen a few recently collected specimens of *B. phalarosoma* and both living and preserved specimens of *B. capitana*. Recently many specimens of *B. hypacra* and *B. nicefori*, previously known from their holotypes, have been collected, and living and preserved specimens have been studied. Species which remain poorly known include *B. palmata* and *B. pandi*, the latter known only from the holotype. Further comments in this paper will be focused on the newly described species and their relatives.

Members of the *sima* group share similarity in size, webbing and other features of their hands and feet, head proportions, and coloration. *Bolitoglossa silverstonei* has more teeth than the other three members of the group, and has a broader foot than either *B. chica* or *B. biseriata*. It is larger than *B.*

chica. In South America the group is restricted to the wet forest west of the Cordillera Occidental, but *B. biseriata* is widely distributed in Panamá. All species of the group are restricted to the lowlands, below 1000 m.

Members of the *medemi* group share similarities in proportions, dentition and coloration. *Bolitoglossa medemi* and *B. ramosi* form one subgroup, and *B. walkeri* and *B. equatoriana* another. The former pair are similarly proportioned and have generally similar color patterns. Both have extensively webbed feet with reduced phalangeal numbers and flattened digits. The feet of *B. ramosi* are smaller and much less well developed than those of *B. medemi*. *Bolitoglossa walkeri* and *B. equatoriana* are somewhat more generalized than the other species pair. *Bolitoglossa walkeri* has the least webbing, the most discrete digits, and the most highly developed phalanges of any species of the group. It has a somewhat narrower head than *B. equatoriana*, and there are some color differences, but otherwise the species are similar. While all members of the *medemi* group are allopatric, only *B. walkeri* lacks sympatric associates. *Bolitoglossa walkeri* and *B. ramosi* occur at about 2000 m elevation, and the other species are lowland forms of the Chocó and the Amazonian basin.

The description of these five species brings the total number of species of *Bolitoglossa* known from South America to 21, and another, *B. taylori*, occurs nearly on the Colombian border in Panamá. Of these, three (*equatoriana*, *peruviana*, *altamazonica*) are extensively webbed, lowland Amazonian species, six (*medemi*, *silverstonei*, *phalarosoma*, *biseriata*, *chica*, *sima*) are extensively webbed, lowland Chocoan species, and three (*hypacra*, *valleculea*, *adspersa*) are generalized, slightly webbed upland species from the Cordillera Occidental, Cordillera Central, and Cordillera Oriental, respectively. The remaining species range from diminutive, specialized highland species (*orestes*) to giant species of intermediate elevation (*capitana*), and the degree of diversity is relatively great. Many species inhabit cloud forest formations, and it is these areas that are likely to produce additional populations. While some of the generalized species are terrestrial, most species are occasionally to almost exclusively arboreal. Species known to occur in bromeliads include *B. nicefori*, *B. savagei*, *B. ramosi*, *B. valleculea*, *B. borburata*, and *B. walkeri*, and most, if not all, of the lowland species are arboreal.

Recent field work has disclosed that sympatry, unknown in 1963, occurs in the following combinations: *B. medemi*-*B. phalarosoma*, *B. valleculea*-*B. ramosi*, *B. peruviana*-*B. equatoriana*, and *B. sima*-*B. chica*. We can expect future field work to yield much additional information concerning ecology and distribution, and, doubtless, new populations and undescribed species will be found.

The five groups of South American *Bolitoglossa* present a rather broad array of species. The *adspersa* group is diverse and its species are allopatric, distributed broadly across Colombia to Panamá, Venezuela, and Ecuador. The *sima* and *phalarosoma* groups are specialized lowland forms of the wet

northwestern forests. The *medemi* group is rather broadly distributed, ecologically and geographically, with species in the uplands in areas of Caribbean and Pacific drainage, in the Chocó, and in the Amazonian Basin. Finally, the *altamazonica* group has the most peripheral distribution within the genus, mostly within the Amazonian Basin.

RESUMEN

En el presente reporte se describen nuevas especies de salamandras pleto-
dóntidas para América del Sur y Panamá. *Bolitoglossa medemi* es una
especie de color oscuro con manos y pies grandes y extensivamente palmeados
y con la cabeza ancha. Se le conoce en varias localidades en el noroeste de
Colombia y en el sudoeste de Panamá, donde se le encuentra entre 50 y 800
m. de elevación. *Bolitoglossa ramosi* es una especie de menor tamaño, de
color mas claro, con manos y pies pequeños, pero tambien extensivamente
palmeados, y con la cabeza ancha. Esta especie es simpátrica con *Bolito-
glossa valleculea* en la Cordillera Central al este de Medellín, Colombia, a
altitudes de aproximadamente 1930 m. *Bolitoglossa silverstonei* es una especie
delgada, de larga cola y color claro, las manos y los pies son anchos y extensi-
vamente palmeados y la cabeza es moderadamente ancha. Ha sido encontrada
solo en una localidad cerca de Quibdó, a una altura de 400 m., en el noroeste
de Colombia. *Bolitoglossa walkeri* no tiene las extremidades tan palmeadas y
generalmente posee menos dientes maxilares que las otras especies. El color
es oscuro en el dorso y claro en el vientre. Se le encuentra a elevaciones de
cerca de 2000 m., cerca de Calí, Colombia. *Bolitoglossa equatoriana* tiene
extremidades más palmeadas que *B. walkeri*, pero tiene como esta última, un
numero bajo de dientes y la misma coloracion. Es simpátrica con *B. peruviana*
en localidades de una elevación de aproximadamente 260 m. en la Amazonía
ecuatoriana. La descripción de estas nuevas especies permite una reevaluación
de las relaciones sistemáticas entre los miembros sudamericanos del género
Bolitoglossa. Se discuten además los caracteres usados en el análisis siste-
mático de veintidós especies y se reconocen cinco grupos de ellas. Los grupos
palmata y *altamazonica* son divididos. *B. silverstonei* es incluida en el nuevo
grupo *sima*, junto con *B. sima*, *B. chica* y *B. biseriata*. Las otras especies
nuevas son los únicos miembros del grupo *medemi*.

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